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The integration of straight contours (snakes and ladders): The role of spatial arrangement, spatial frequency and spatial phase

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ABSTRACT

In the present study we addressed the issue of whether the Gestalt principle of grouping by similarity (iso-orientation) subtends extraction of straight contours made up of disconnected, iso-oriented Gabor elements, whether collinear (snakes) or parallel (ladders). To prevent the use of the most obvious grouping principle of good continuation, which allows us to perceive the relation between local and global orientation along the contour, we manipulated the spatial arrangement of randomly oriented Gabors in the background: they were positioned on an ordered grid, and grouped on the basis of good continuation, or randomly positioned and not grouped. Grid-positioned backgrounds exert a suppressive contextual influence on detection of good continuation along the contour path. Results obtained in a two-interval forced choice task showed that the orderly-positioned background did not completely prevent detection of snakes and ladders. Detection of snakes was hampered at low spatial frequency whereas detection of ladders was improved by the randomly-positioned background at high spatial frequency. These contextual influences support the suggestion that both iso-orientation and good continuation rules are employed by the association field underlying the binding of straight contours. In addition, they are not compatible with integration of snakes and ladders elements within a single receptive field. In support of this suggestion we found that phase constancy within contour elements (as opposed to phase randomization) improved snake detectability at low spatial frequency, and, unexpectedly, impaired ladder detectability at high spatial frequency. This suggests that a low-level mechanism based on the balance between excitatory and inhibitory lateral interactions at a first stage may account for the detection of both straight contours.

1. Introduction

To recognize a contour made up of disconnected elements, these elements have to be correctly linked together and segmented from those not belonging to the contour. Since linked elements are locked in their orientation (local) to the curvature of the whole contour path (global), they respect the Gestalt law of "good continuation." This law states that discrete contour elements, positioned and oriented along a smooth path, are readily grouped together into a salient contour by a process that establishes a relationship between local and global orientation (Rock & Palmer, 1990; Wertheimer, 1938). Field, Hayes, and Hess (1993) formalized the "good continuation" law in the "association field" model, according to which binding follows a joint constraint of position and orientation (Hess & Field, 1999).

The association field model does not include specific postulations to account for a combination of good continuation with another Gestalt rule (Koehler, 1928) of grouping, that of "similarity." This rule is optimally expressed within straight contours made up of iso-oriented (and thus similar) elements with either a collinear (snakes) or a parallel arrangement (ladders). Similarity may indeed play a role, together with good continuation, in the integration of straight contours and could account for three well-documented findings. The first is that straight contours made up of iso-oriented elements are more salient than curvilinear ones (Field, Hayes, & Hess, 1993; Hess & Dakin, 1997, 1999; Ledgeway, Hess, & Geisler, 2005). The second is that, although ladders made up of parallel elements do not respect the joint constraint of position and orientation, they are still well detected (Bex, Simmers, & Dakin, 2001; Hansen & Hess, 2006; Ledgeway, Hess, & Geisler, 2005), and this could be because the elements in a "ladder" contour are iso-oriented. The third is that snakes are more salient than ladders (Bex, Simmers, & Dakin, 2001; Field, Hayes, & Hess, 1993; Ledgeway, Hess, & Geisler, 2005; May & Hess, 2008, 2007a) and this may be because snake contours are defined by both iso-orientation and collinearity of the elements (Casco et al., 2009; Kapadia et al., 1995; Li & Gilbert, 2002).

In the present study we asked two questions. The first is whether straight contours are more salient than is predicted by

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the classical association field because they involve grouping by similarity (iso-orientation) in addition to grouping by good continuation. We addressed this question by manipulating the spatial arrangement of the elements in the background (Polat & Bonneh, 2000), thus introducing a contextual factor into contour integration. Indeed, we positioned the elements of the background on a grid. This way they are perceived as grouped into stripes regardless of their orientation (Bozzi, 1969, 1989; Wertheimer, 1938). This role of "pure" good continuation on grouping has been described by Gestalt psychologists (Bozzi, 1969, 1989; Wertheimer, 1938) who have thought it the spatial analogy of common fate (Bruce, Georgeson, & Green, 2003) and its neurophysiological correlate could rely on the physiological connections between pairs of neurons of all relative orientation preference (Das & Gilbert, 1999). We expected the grouping of randomly oriented background elements into stripes to have a strongly suppressive contextual effect on detection of the target "stripe," i.e. the straight target contour. Note that this effect should not be confused with recently discovered local contextual effects in contour integration (Dakin & Baruch, 2009; May & Hess, 2007b; Robol, Casco, & Dakin, 2012; Schumacher, Quinn, & Olman, 2011).

We set two background conditions: (1) the background elements were randomly positioned, with the target contour distinguished by both good continuation and the similarity of its elements, (2) background elements were positioned orderly in a grid, and detection only occurred because of similarity. We predicted that if only good continuation underlies detection (as with curvilinear contours), the contextual effect of the orderly-positioned background should prevent detection. Alternatively, if both grouping rules, good continuation and similarity, were used by the association field we predicted the orderly-positioned background would reduce but not prevent detection.

The second question that we addressed is whether integration of straight contours occurs within a receptive field or across receptive fields. It has indeed been suggested that facilitatory interactions within one receptive field may account for detection of iso-orientation in ladders (Graham & Wolfson, 2004) and snakes (Levi & Waugh, 1996; Yu & Levi, 1997). Other authors instead suggest that the substrate for contour integration may be contextual interactions and intrinsic horizontal connections in the primary visual cortex (Li & Gilbert, 2002). The comparison of the contextual effects produced by the two types of background may allow us to distinguish between these two explanations. Indeed, contextual influence of the orderly-positioned background is not easily accounted for by the influential models of straight contours detection which assume that integration occurs within one high-level filter (Hess & Dakin, 1997, 1999; May & Hess, 2008, 2007b). These mechanisms may respond to feature contrast (Graham, 2011) in the center and the surround of their receptive field (mainly to orientation but also to contrast polarity and spatial frequency), regardless of the spatial arrangement of these features. A suppressive contextual effect exerted by the regular background would instead be compatible with integration based on intrinsic long-range horizontal connections. These connections are formed in V1 by axons of pyramidal cells and linking neurons with non-overlapping receptive fields and the same orientation preference (T'so & Gilbert, 1988; T'so, Gilbert, & Wiesel, 1986). These connections are mostly excitatory for both collinear (Kapadia et al., 1995) and parallel receptive fields (Fitzpatrick, 1996; Mitchison & Crick, 1982; Rockland & Lund, 1982, 1983), but inhibitory interactions between iso-oriented parallel elements are also possible (McGuire et al., 1991; Polat, 1999; Zhaoping, 1998).

In addition, to explore further the role of lateral interaction in straight contour integration we manipulated the phase of the elements in the target. Other studies have manipulated contour elements to this end by varying inter-element distance and element density (Li & Gilbert, 2002; Polat, 1999; Polat & Bonneh, 2000) and also phase (Bell et al., 2011; Williams & Hess, 1998). In particular, binding of disconnected elements to curvilinear contours is not strongly affected by phase manipulation (Field, Hayes, & Hess, 2000), supporting the view that this operation involves high-level visual processes. Facilitation by collinearity in contrast detection tasks also shows relative phase insensitivity in some conditions (Chen & Tyler, 1999; Wehrhahn & Dresp, 1998; Yu & Levi, 1997). Other studies, however, have shown a strong effect of phase in detection of aligned iso-oriented micropatterns, leaving open the possibility that although phase does not play a role in integration of smoothly curved paths it could affect integration of straight paths (Williams & Hess, 1998). Our hypothesis is that, if manipulating phase (and spatial organization in the background) produces an effect on snake and ladder detection, this would suggest that integration, based on good continuation and similarity, involves intracortical lateral interactions at early level filters (Bonneh & Sagi, 1998a). Phase insensitivity and absence of contextual effects would instead support integration within a single receptive field of second-stage filters after rectification of first-stage filters (Chen & Tyler, 1999; Usher et al., 1999).

2. Experiment 1

Experiment 1 compares detection of straight contours embedded in a surround of either randomly-positioned elements or elements positioned on an orderly grid (orderly-positioned).

2.1. Methods

2.1.1. Subjects

One author and five naïve subjects served as observers in Experiment 1. Observers sat in a dark room and were placed 57 cm from the screen. Viewing was binocular. They were given initial training to familiarize themselves with the stimuli and the task. All subjects had normal or corrected-to-normal visual acuity. Subjects participated voluntarily with no compensation and gave their informed consent prior to their inclusion in the experiment.

2.1.2. Apparatus and stimuli

Stimuli were displayed on a 19-in. CTX CRT Trinitron monitor with a refresh rate of 60 Hz and generated with Matlab Psychtoolbox (Brainard, 1997; Pelli, 1997). The screen resolution was 1280×1024 pixels. Each pixel subtended ~1.9 arcmin. The mean luminance was 32 cd/m^2. Luminance was measured with a Minolta LS-100 photometer. Stimuli were presented within a square window ($10 \times 10^\circ$) placed at the center of the screen. Each stimulus was generated anew immediately prior to its presentation and consisted of a dense spatial array of 100 Gabor patches. Each Gabor was defined as follows:

$$G(x,y) = m * \sin(2\pi f_x x\pi + \varphi) * \exp\left(-(x^2+y^2)/\sigma^2\right) \quad (1)$$

where m is the modulation depth of the sinusoidal carrier, f_x is the spatial frequency (SF), φ is the phase of the carrier (0°). The Gaussian is expressed by the exponential part of Eq. (1): x and y are, respectively, the horizontal and the vertical distance from the peak of the Gaussian, whereas σ is the standard deviation (0.21°). The contrast was fixed at 0.5 (Michelson contrast).

Gabor patches were placed within a raster of 10×10 cells (each cell was $1 \times 1^\circ$) (see Field, Hayes, & Hess, 1993). Each Gabor patch occupied a single cell. The target path was made up of five elements with orientation either parallel (snake, Fig. 1, Panel A) or orthogonal to the global orientation of the path (ladder, Fig. 1, Panel B). In addition, the path could be either horizontal or vertical.

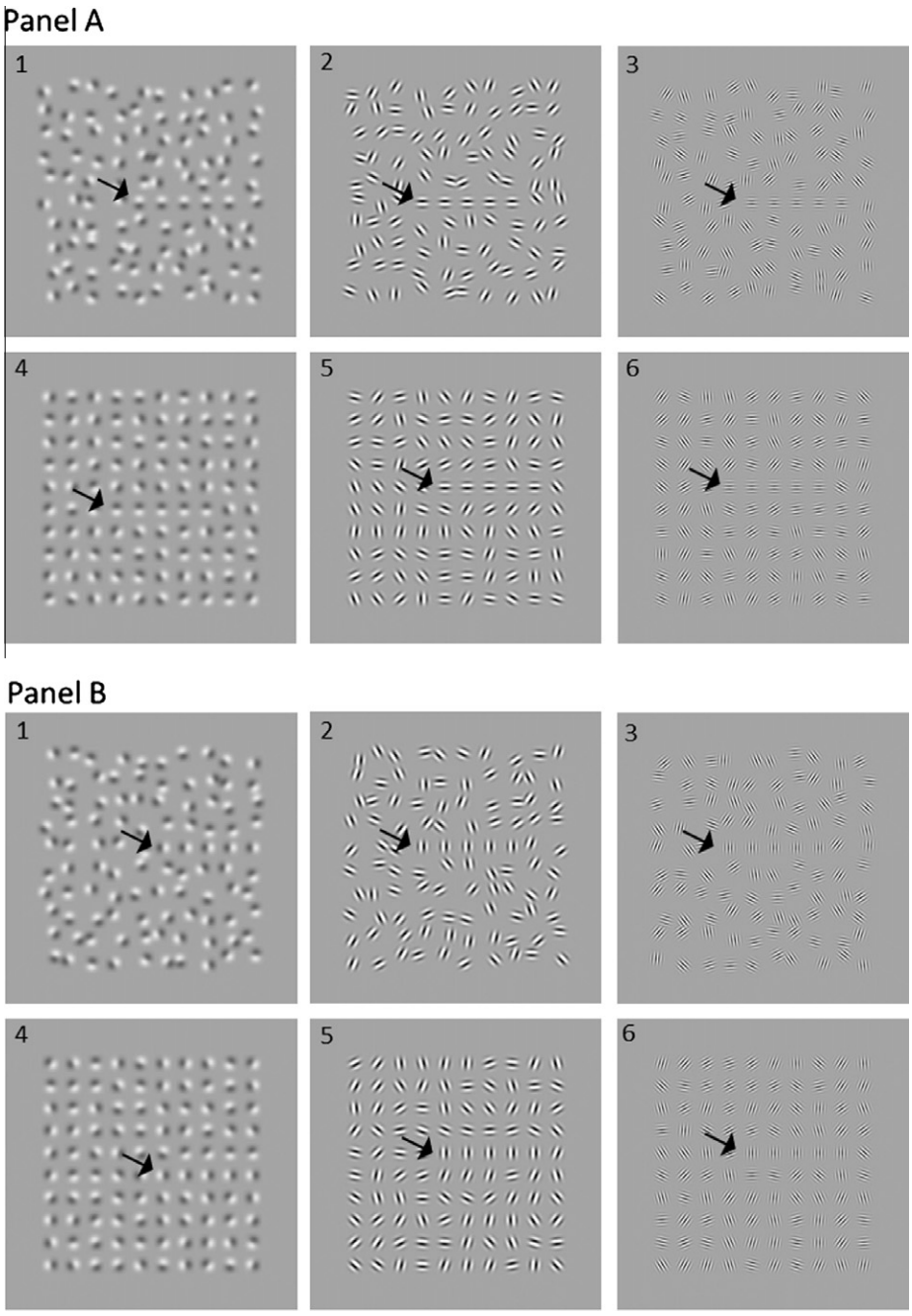

Fig. 1. Fig. 1 shows the stimuli used in Experiment 1. The elements forming the contour (indicated with the arrows) were orderly positioned and had a constant phase and the same orientation (either parallel to the path: snake [Panel A] or orthogonal to the path: ladder [Panel B]). The elements in the background had random position and orientation (randomly-positioned background condition [Panel A and B, from 1 to 3]). Panels A and B from 4 to 6 show the stimuli used in the orderly-positioned background condition. The three spatial frequencies tested (1 cpd, 3 cpd and 6 cpd) are shown in columns. In the experiment, the vertical contour was also presented. For demonstrative purposes, the figures show stimuli with an exaggerated contrast.

Thus, snake paths were defined by elements with the same element and path orientation, whereas ladders were defined by elements with the same orientation but orthogonal to the path's orientation. The background elements had a random spatial orientation (ranging from zero to 360°). In addition, they could be either orderly positioned on a grid (orderly-positioned condition, Fig. 1, bottom row in Panel A and Panel B) or positioned randomly, by spatially jittering their ordered position in a random direction (ranging from zero to 360°) with respect to the center of the cell by 0.3° (randomly-positioned condition, Fig. 1, top row in Panel A and Panel B).

In the latter condition, Gabors could slightly overlap, one occluding the other without summing their luminance profile; in this way we prevented changes in luminance to create cues.

In the case of the randomly-positioned condition, mean luminance and contrast of the Gabor patches were the same even when they slightly overlapped. Distance between elements was 1° (center-to-center distance) and on average it was maintained approximately constant in the randomly-positioned condition as well. Also, since the background elements were randomly oriented, the context did not create specific spatial cues for either ladder or snake paths.

2.1.3. Procedure

A two-interval forced-choice (2IFC) procedure was used. In each trial observers were required to choose which of two temporal intervals (followed by 100 ms mask and an Inter-Stimulus-Interval [ISI]: 100 ms) contained the target path. For example, the target path, either a snake or a ladder, was presented in the first interval embedded in the background whereas, in the second interval, only the background was displayed, or vice versa. The interval in which the target path appeared was randomized across trials. During the ISI, the screen was set to the mean luminance (32 cd/m^2). In order to reduce the spatial uncertainty of the target path, it was displayed and constrained to lie within a central squared region of the stimulus window ($7.5 \times 7.5^\circ$). The orientation of the whole path (i.e. vertical vs. horizontal), the stimulus type (snake vs. ladder) and the duration of each interval (from 50 to 300 ms: 50 ms step) were varied within each block. The type of background (i.e. orderly- vs. randomly-positioned) and the SF (1, 3 and 6 cpd) were varied across blocks.

For each interval the stimulus was immediately followed by a mask made up of a raster of Gabor patches with random orientation, random phase value and either aligned (in the orderly-positioned condition) or spatially jittered (in the randomly-positioned condition). There were a total of 52 conditions: 2 background conditions $\times$ 2 types of target path (i.e. snake vs. ladder) $\times$ 6 stimulus exposures (from 50 to 300 ms: 50 ms step) $\times$ 3 spatial frequencies (i.e. 1 cpd vs. 3 cpd vs. 6 cpd). Observers performed 32 repetitions per condition.

Individual performances of three subjects in a pilot experiment conducted with Gabor patches with a spatial frequency of 1 cpd were used to estimate the appropriate range of exposures that would avoid ceiling and floor effect.

A logit function (Berkson, 1953; Chatterjee & Price, 1977) was fitted to the data in order to estimate the thresholds, defined as the exposure level at which observers detected the target path with a probability of 0.75. The two psychometric functions, describing accuracy as a function of exposure (ranging from 20 ms to 640 ms) separately for snakes (continuous line, Fig. 2) and ladders (dashed line, Fig. 2), showed a proportional increase in accuracy from 50 ms to 300 ms. Thresholds were higher for the three subjects in the ladder condition (171.1 ms for subject CV, 283.1 ms for subject NL and 311.1 ms for subject CO) than in the snake condition (89.36 for subject CV, 158.7 ms for subject NL and 221.7 ms for subject CO). Moreover, the two psychometric functions had similar slopes (0.008 with snakes and 0.005 with ladders for observer CV, 0.006 and 0.004 for NL, 0.003 and 0.001 for CO), indicating that the difference between the two contours was constant over a range of exposures. Thus, for all the subjects, performance increased proportionally with duration. These exposure levels were taken as the range to be used in the following experiments.

2.1.4. Results and discussion

Results from Experiment 1 are illustrated in Fig. 3. Overall, the results show that detection of snakes is high for all the SFs in the condition where background elements are randomly positioned and improves gradually with increasing SF in the regularly-positioned background. Thus, the detection of snakes is more accurate with the randomly-positioned background only at low SF. For ladders, instead, detection is very impaired at low SF in both the background conditions, and improves more with increasing SF in the orderly-positioned condition. At the highest SF, ladder detection is better with the randomly-positioned background. Since detection increases proportionally with the spatial frequency employed (Fig. 3), only the results with the highest and the lowest spatial frequency were analyzed for better assessment of this effect.

The complex dissociation of the effect of the background on the detection of snakes and ladders was pointed out by two-way repeated-measures ANOVAs with Background Type (orderly- vs. randomly-positioned) and Exposure (100, 150, 200, 250, chosen to reduce ceiling and floor effects) as factors. ANOVAs were run separately for the two contour types and two spatial frequencies (1 and 6 cpd).

For snakes, besides the significant effect of exposure at high SF ($F_{(3,5)} = 18.431$, $p = 0.004$), the predicted influence of the background was revealed by a significant effect of this main factor ($F_{(1,5)} = 9.532$ and $p = 0.027$) at low SF and by a significant Background $\times$ Exposure interaction ($F_{(3,5)} = 4.428$, $p = 0.038$) at high SF. In the latter the randomly-positioned background only improves performance at an exposure duration of 250 ms (Bonferroni corrected *t-test*, $p = 0.025$). Conversely, for ladders, a main effect of Background type was only present at 6 cpd ($F_{(1,5)} = 16.286$, $p = 0.010$). The effect of exposure was also significant at both low ($F_{(3,15)} = 8.288$, $p = 0.008$) and high ($F_{(3,15)} = 12.950$, $p = 0.001$) SF. None of the other main effects or interactions were significant.

Considered together, the results of Experiment 1 confirmed that both snakes and ladders are very salient even at short exposures (Ledgeway, Hess, & Geisler, 2005; May & Hess, 2007a). The new finding is a different effect of the grid-positioned background on snake and ladder detection specific to the spatial frequency tested:

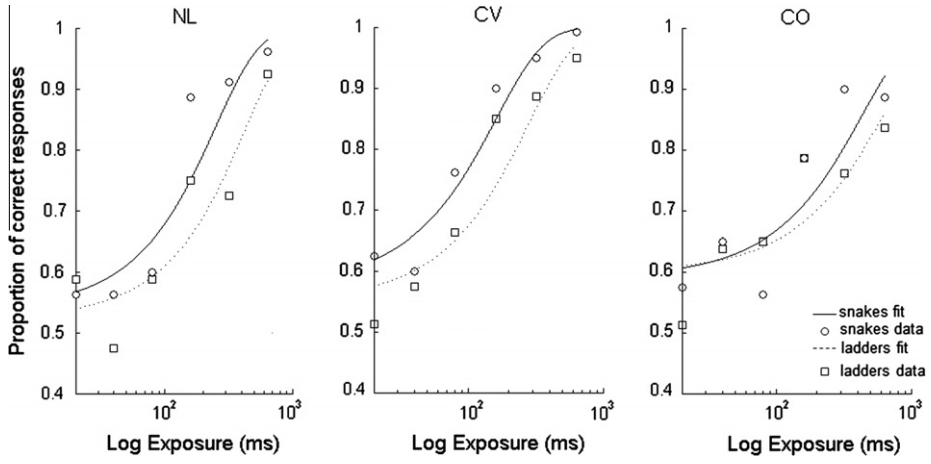

Fig. 2. Individual psychometric functions of the three subjects participating in the preliminary study. Circles refer to snake detection and squares refer to ladder detection. Stimuli were randomly presented at 20 ms, 40 ms, 80 ms, 160 ms, 320 ms and 640 ms. As expected, performance increased as a function of the exposure in both the conditions.

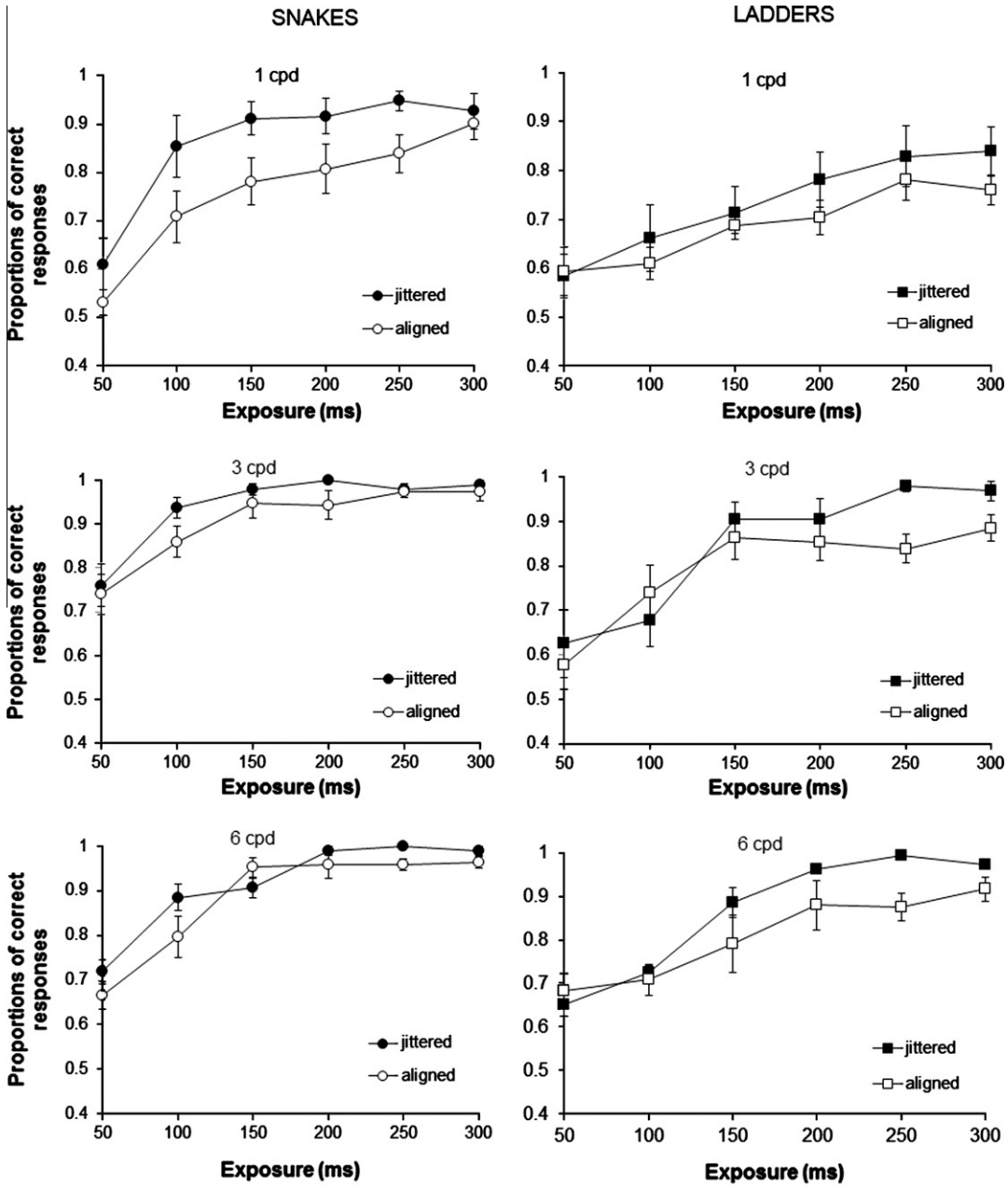

Fig. 3. Results of Experiment 1. Proportions of correct responses were plotted as a function of the exposures. The solid symbol refers to the randomly-positioned background condition and the empty symbol to the orderly-positioned background condition. Results for snakes and ladders are shown in the left and right column, respectively. The three spatial frequencies used were plotted separately (1 cpd in the top row, 3 cpd in the middle row, 6 cpd in the bottom row). SEs are plotted for each data point.

snake contours are impaired by the orderly grid-positioned background at a low spatial frequency, whereas ladder contours are more salient with the randomly-positioned background, at a high spatial frequency.

3. Experiment 2

Whereas binding of curvilinear contours is little affected by phase manipulation (Field, Hayes, & Hess, 2000), some studies have reported a strong effect of phase on collinear facilitation (Williams & Hess, 1998). If phase played a role, this would suggest that detection occurs at the level of first-order filters before a full-wave rectification of the output (Chen & Tyler, 1999) and that lateral interactions between them may occur (Bonneh & Sagi, 1998).

The role of phase was investigated with the two types of background, since phase randomization of elements in the target path may interact differently with the contextual influences of randomly-positioned and grid-positioned background elements.

3.1. Observers

The same observers who took part in Experiment 1 participated in Experiment 2.

3.2. Apparatus and stimuli

The general method used in this experiment was identical to that employed in Experiment 1, with the exception that the

elements in the target path could assume, randomly, two phase values. To produce Gabors with randomly alternated phase, the phase value of each element in the path was randomly assigned between 0° or 180°. Gabors in the path had the same orientation, as in Experiment 1, either forming a snake (Fig. 4, Panel A) or a ladder contour (Fig. 4, Panel B). The same two background conditions of Experiment 1 (i.e. randomly- vs. orderly-positioned) were used (Fig. 4).

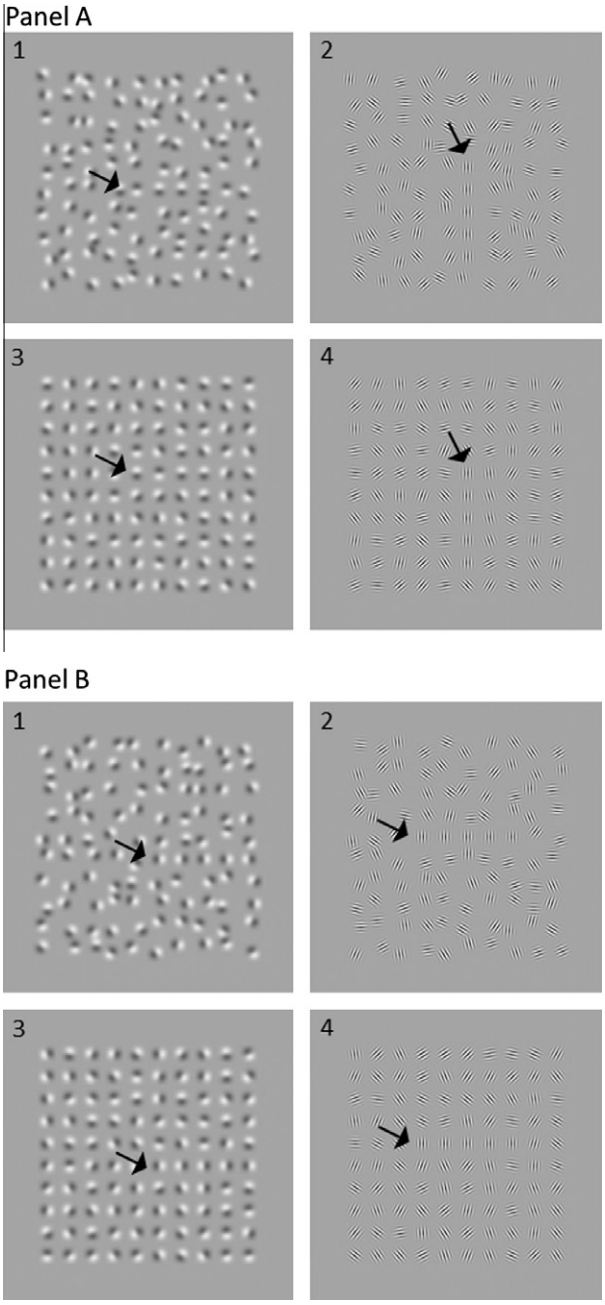

Fig. 4. Examples of the stimuli used in Experiment 2 (random phase condition). The elements forming the contour (indicated by arrows) had regular positions and they all had random phases and the same orientation. Both snakes (Panel A) and ladders (Panel B) were presented. In the random-positioned background condition, the elements in the background had random position and orientation (Panels A and B, Figs. 1 and 2). In the orderly-positioned background condition (Panels A and B, Figs. 3 and 4) the elements in the background had random orientation and regular position. The two spatial frequencies tested (1 cpd and 6 cpd) are shown in columns. The contours could be either vertical or horizontal. For demonstrative purposes, the figures show stimuli with an exaggerated contrast.

3.3. Procedure

The same procedure as in Experiment 1 was used. We tested the SFs of 1 and 6 cpd.

3.4. Results and discussion

Results from Experiment 2 are shown in Fig. 5. The main finding is that phase randomization selectively impairs snake detection at low spatial frequency. Conversely, ladder detection shows no effect at low spatial frequency and it slightly but significantly improved at high spatial frequency when phase is randomized. Moreover, this effect was present for all the exposures tested. We confirmed these observations by means of three-way repeated measure ANOVAs with Phase (constant, Experiment 1 vs. random, Experiment 2), Background Type (randomly- vs. orderly-positioned), and Exposure (100, 150, 200, 250 ms) as factors. Analyses were run separately for snakes and ladders and for 1 cpd and 6 cpd.

For snakes, we found a significant effect of Phase ($F_{(1,5)} = 56.131$, $p = 0.001$) only at low SF. As in Experiment 1, we found an effect of Background ($F_{(1,5)} = 35.559$, $p = 0.002$) at low SF and a significant interaction Exposure × Background Type ($F_{(3,15)} = 4.358$, $p = 0.039$) at high SF, showing that performance increased with the random background only for the highest duration of the stimulus ($p = 0.030$, Bonferroni corrected *t-tests*). Not surprisingly, we found a significant effect of Exposure, both at low ($F_{(3,15)} = 10.421$, $p = 0.001$) and high ($F_{(3,15)} = 23.445$, $p = 0.002$) SFs.

ANOVAs on ladders also revealed a different pattern of results at low and high spatial frequency. Indeed, we only found a significant effect of Exposure when testing 1 cpd ($F_{(3,15)} = 8.962$, $p = 0.008$), whereas the three principal effects were found at high spatial frequency (Phase, $F_{(1,5)} = 10.970$, $p = 0.021$; Background, $F_{(1,5)} = 19.694$, $p = 0.007$; Exposure, $F_{(3,15)} = 22.295$, $p = 0.0001$), showing an increase in detection with, interestingly, randomized phase, random background and increase in exposure duration. None of the other main effects or interactions were significant.

Taken together, the results revealed that phase manipulation selectively reduces snake detection, but only when the spatial frequency tested is low (i.e. 1 cpd). It also improves ladder detection at high spatial frequency for both the backgrounds tested. Note that previous studies on contour binding failed to show severe impairment in detection as a consequence of phase randomization (Bex, Simmers, & Dakin, 2001; Field, Hayes, & Hess, 1993, 2000; Hess & Dakin, 1999).

4. General discussion

To summarize, the results showed that detection of snakes defined by Gabors with low spatial frequency carriers was hampered by orderly-placed background elements in a grid. Overall, ladders were less salient than snakes and, when defined by Gabors with high spatial frequency carriers, their detection was improved by random positioning of the background. Moreover, regardless of the spatial organization of the background, snake detectability increased solely because of phase constancy, specifically at low spatial frequency, whereas ladders were slightly but consistently improved by phase randomization.

We discuss the combined effect of phase randomization and spatial arrangement of background separately for snakes and ladders, with the aim of determining whether the integration of iso-oriented elements into the two types of contours can be accounted for by lateral interactions between local elements.

Note that we assume that interference may occur between mechanisms with the same response properties operating at the same stage of processing, either at the first or at a higher level.

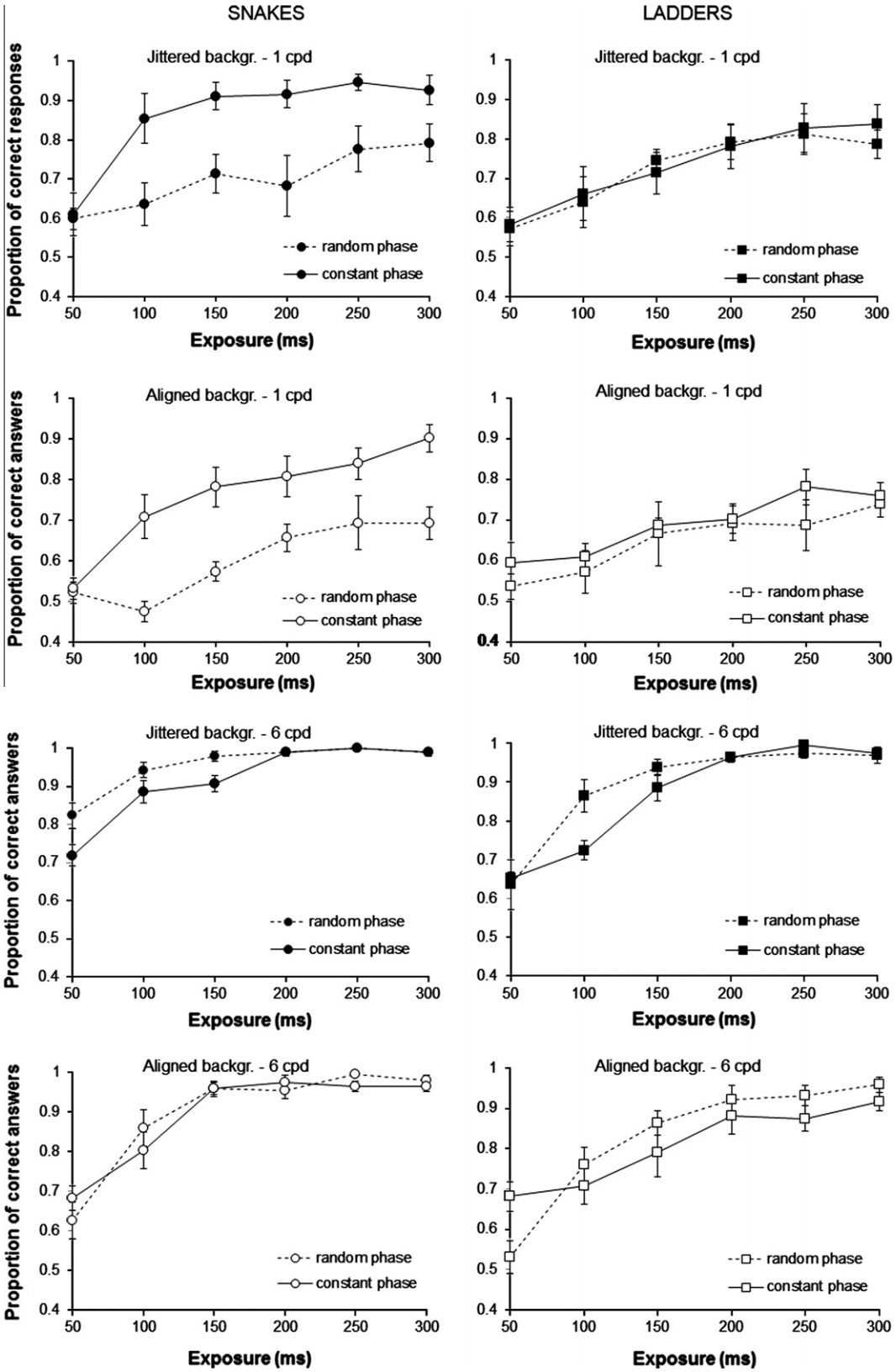

Fig. 5. Results of Experiment 2. Proportions of correct responses are plotted as a function of the exposures. SEs are plotted for each data point. In different rows, data for the comparison between the constant-phase condition (continuous line) and the random-phase condition (dashed line) are shown. The solid symbol refers to the randomly-positioned background condition and the empty symbol to the orderly-positioned background condition. Results for snakes and ladders are shown in the left and right column, respectively. The two spatial frequencies used were plotted separately (1 cpd in the top, 6 cpd in the bottom).

4.1. Snakes

Detection of snakes could in principle be accounted for by integration within a single receptive field, either at a first or at a second stage. Our findings, however, do not support this view. Integration within a single second-stage receptive field is, on the one hand, not compatible with the phase effect, when this filter is fed by the full-way rectified output of first-order filters. On the other hand, the output of a second-stage filter fed by the output of half-way rectified first-stage filters would be affected by phase perturbation (Motoyoshi & Kingdom, 2007). This filter, however, would be insensitive both to iso-orientation, because it integrates across different carrier orientations (Motoyoshi & Kingdom, 2007), and to the spatial arrangement of the background where the random orientation and phase produce zero output in this mechanism.

At a first stage, low spatial frequency Gabors forming the straight contour optimally stimulate a detector of luminance gradient with odd receptive field, provided that the dark region of the Gabor patch falls onto the inhibitory portion of the receptive field and the light one onto the excitatory portion. Obviously such a mechanism does not respond to a contour made up of phase randomized Gabors, and indeed we found that at low stimulus duration where scrutiny and eye movements are not allowed detection probability is far below 0.75 (the threshold value). In addition, such a first-stage filter returns zero output in the background where elements are randomly oriented, a fact which is incompatible with the impairment owing to the spatial arrangement of the surround elements orderly positioned on a grid.

An interesting model which could account for the failure in detecting snakes, when the phase is randomized, is that which assumes the activation of first-stage luminance filters that use position as the feature involved in contour processing (Prins, Kingdom, & Hayes, 2007). This mechanism assesses the shape of the straight contour based on the local positions of Gabors with the same phase. Several researches (Dakin & Hess, 1999; Hansen & Hess, 2007; Phillips & Todd, 2010) have pointed out the importance of phase alignment, especially in terms of texture discrimination. In the randomized phase condition this mechanism may produce local tilts, since it is possible that the phase of the Gabor carrier affects its perceived location. Randomizing the phase of the Gabor would then introduce positional noise and make it more difficult to perceive the collinearity of elements in the straight snake. A mechanism using position as a feature involved in contour processing is not sensitive to local orientation (Prins, Kingdom, & Hayes, 2007) and this could explain the detrimental effect on detection when, in an ordered-grid background, the only cue is orientation gradient. The manner in which this mechanism assesses the shape of the straight contour based on the local position of Gabors with the same phase has not been determined yet. It cannot be ruled out that this occurs through lateral interactions between first-stage mechanisms with the same phase (Roncato & Casco, 2006, 2009) that have been shown to be extremely good at detecting relative position (Watt & Andrews, 1982).

4.2. Ladders

Detection of ladders fails at low spatial frequencies regardless of phase constancy and background spatial arrangement. Ladders are detected rather when defined by high spatial frequency Gabors, particularly when the background elements are randomly positioned and the phase of elements in the contour is random. The inability to detect low spatial frequency ladders is particularly evident at short stimulus duration (detection probability is below 0.75, the threshold value). The improvement by phase randomization excludes the possibility that detection can be accounted for by an integration mechanism within a single first-stage receptive field. It has been suggested that these contours could be detected by second-stage sign-opponent mechanisms (Graham & Sutter, 1998; Graham & Wolfson, 2004). May and Hess (2007b, 2008) and Hess and Dakin (1997, 1999) suggested that ladder detection is based on a second-stage filter fed by first-stage filters orthogonally oriented to the second-stage filter. It is difficult, however, to explain how the response of these mechanisms is affected by the spatial arrangement of the background. Even more difficult is it to account for the phase effect at high-spatial frequencies. There is no obvious reason why phase randomization should improve the response of a sign-opponent mechanism.

A more plausible explanation is provided by models based on spatial interactions between filters with parallel receptive field axes, mediating ladder detection (Yen & Finkel, 1998). These interactions are not only weakly facilitatory (Sarti, Citti, & Petitot, 2009) but also inhibitory (Polat, 1999; Zhaoping, 1998), thus accounting for the reduced saliency of ladders with respect to snakes (Yen & Finkel, 1998).

We suggest that inhibition by lateral interactions amongst ladder elements could be reduced by phase randomization. It has been shown that crowding is reduced when target and flankers have different contrast polarity (Chakravarthi & Cavanagh, 2007). One could assume that there are inhibitory lateral interactions amongst parallel elements that produce a form of crowding and they weaken the link between adjacent contour elements. This interpretation would explain why random phase improves detection, i.e. it may induce a release in reciprocal crowding amongst target elements.

Our results with ladders are hence not trivial, because they seem to refute the most common explanation of ladder contour integration based on the response of a second-stage filter and instead support an interpretation based on lateral interactions between first-order filters.

Combining the findings on snakes and ladders, we can see that a mechanism based on the balance between excitatory and inhibitory lateral interactions may account for the detection of both the contours. Yen and Finkel (1998) proposed an associative field that binds together the adjacent elements with the same orientation, either co-axial (for snakes) or trans-axial (for ladders). The co-axial connections are assumed to be stronger than the trans-axial ones. This model accounts for both the detection of snakes and ladders, but predicts stronger integration for snakes, possibly because of high facilitatory lateral interactions, and less strong integration for ladders, possibly caused by a balance between facilitation and inhibition. A mechanism with these features seems to be the most parsimonious to account for the detection of straight contours.

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